RESEARCH ARTICLE `OPEN ACCESS`

The Phylogenetic Architecture of Recruitment Networks

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ABSTRACT

Aim: Plant recruitment involves both stochastic and deterministic processes. Recruits may establish independently or interact nonrandomly with canopy plants. We explore this deterministic aspect by testing whether recruitment patterns are influenced by the phylogenetic history of canopy and recruiting plants. Since the effect of canopy plants in recruitment can be positive (facilitation), negative (competition) or neutral, we also estimated the phylogenetic signal separately for each interaction type. Furthermore, we assessed whether environmental stress influenced the phylogenetic signal, under the expectation that more severe environmental conditions will lead to stronger phylogenetic signatures in network structure.

Location: Global.

Time Period: 1998–2021.

Major Taxa Studied: Angiospermae.

Methods: We analysed recruitment interactions occurring in 133 plant communities included in the RecruitNet database, which encompasses a wide range of biomes and vegetation types. The phylogenetic signal in canopy–recruit interactions was quantified in different dimensions of the recruitment niche, represented by the level of interaction generalisation, and by the taxonomic and evolutionary composition of the group of canopy plants.

Results: We found significant phylogenetic signals in more networks than expected by chance. Canopies' evolutionary history influenced facilitative and competitive but not neutral interactions. The phylogenetic signal in the recruitment niche strengthened in arid regions, suggesting that stressful habitats promote the occurrence of conserved recruitment interactions where closely related species recruit in association with closely related canopy species.

Main Conclusions: Despite the strong influence of stochastic processes on plant recruitment, evolutionary history plays a significant role in driving the recruitment process, especially in harsh environments. In particular, the historical effect becomes

1 | Introduction

Plant recruitment is a fundamental ecological process that determines plant species distribution and community assembly (Grubb 1977; Grime 2001). Although some plant species can recruit away from other plants (e.g., in vegetation gaps or bare ground), many species depend on the presence of micro-environmental conditions provided by canopy species (i.e., already established plants) to successfully recruit (Pérez-Navarro et al. 2024). These canopy–recruit interactions form complex recruitment networks (Alcántara et al. 2019), and there is increasing evidence that, as in other biological interactions (Gómez, Verdú, and Perfectti 2010), the evolutionary history of the interacting species may be shaping network structure (Alcántara, Garrido, and Rey 2019; Verdú and Valiente-Banuet 2011). This is, in principle, expected, because the functional traits involved in the recruitment process tend to be evolutionarily conserved (Valiente-Banuet and Verdú 2007). Consequently, closely related species are likely to require similar recruitment conditions, and thus to interact with sets of phylogenetically close canopy species (i.e., phylogenetic conservatism of canopy–recruit interactions; Verdú, Jordano, and Valiente-Banuet 2010). However, under conditions of resource limitation, closely related recruiting species may require diverging recruitment conditions to avoid competition (Bulleri et al. 2016; Castillo, Verdú, and Valiente-Banuet 2010). Unveiling the drivers of nonrandom recruitment interactions is important for understanding patterns of plant community assembly (Alcántara et al. 2018), and also for predicting how plant communities will eventually respond to ongoing threats such as anthropogenic disturbances or climate change (Ings et al. 2009; Peralta 2016).

The recruitment niche is composed of the set of environmental conditions provided by canopy plants that are necessary for recruits to successfully establish (Young, Petersen, and Clary 2005). Ultimately, the regeneration niche is determined by the traits of the recruit species that tend to be evolutionarily conserved (Valiente-Banuet and Verdú 2007). Thus, the amount of evolutionary history driving the recruitment process may be reflected in different dimensions of this ecological niche related to the associated set of canopy plants (Figure 1). For example, closely related species may recruit under a similar number of canopy species (i.e., phylogenetic signal in the recruitment niche breadth; Martín González et al. 2015; Rezende et al. 2007; Figure 1a). Additionally, closely related species may recruit under taxonomically similar groups of canopy species (i.e., phylogenetic signal in the taxonomic identity of the canopies; Aizen et al. 2016; Figure 1b), or under evolutionarily similar groups of canopy species (i.e., phylogenetic signal in the evolutionary history of the canopies; Bergamini et al. 2017; Figure 1c). While the former reflects the relevance of particular canopy species within the recruitment network, the latter reveals phylogenetic redundancy in the interactions, which occurs when phylogenetically close canopy species play similar functional roles within the community.

Although incipient evidence exists on the evolutionary conservatism of the interactions in recruitment (Alcántara, Garrido, and Rey 2019) and facilitation (Verdú and Valiente-Banuet 2011) networks, we largely ignore the generality of this pattern. Empirical and simulation studies have identified common network properties that depend on the interaction type, such as increasing modularity and high phylogenetic signals in the interactions in antagonistic networks, and increasing nestedness and lower phylogenetic signals in the interactions of mutualistic ones (Maliet, Loeuille, and Morlon 2020; Rohr and Bascompte 2014). The inherent complexity of recruitment networks, however, makes it difficult to anticipate the magnitude of the phylogenetic signal in the interactions. Canopy species are, in principle, unaffected by the interaction, but eventually, they may suffer a cost or gain a benefit associated with the interaction with recruiting species as these grow up (Maestre et al. 2009; Sortibrán, Verdú, and Valiente-Banuet 2019; Verdú, Jordano, and Valiente-Banuet 2010). In turn, recruiting species may be facilitated by canopy species, compete with them or result unaffected by the interaction (Alcántara et al. 2018). Recruitment networks are, thus, complex networks that can be decomposed into facilitation subnetworks (i.e., networks comprised solely interactions in which canopies promote a positive fitness effect on their recruits), competition subnetworks (i.e., networks composed of canopy–recruit interactions in which canopies have depressing effects on their recruits) and neutral subnetworks (i.e., networks including interactions in which a net fitness effect of canopies on their recruits is absent; Alcántara et al. 2019). If facilitation, competition or neutral recruitment interactions take place with similar frequencies within a single community, opposing effects might result in a recruitment network (RN) with little to no phylogenetic structure.

The phylogenetic signal in recruitment interactions may also vary in space following changes in species composition, because of changes in species abundances and functional traits that may condition the actual realisation of canopy–recruit interactions (Pellissier et al. 2018). In harsh environments, in particular, plant recruitment usually depends on the availability of specific microsites provided by canopy species with specific traits that buffer stressful conditions (Castillo and Valiente-Banuet 2010). In fact, facilitation interactions are common in stressful environments, with stress-tolerant species allowing the recruitment of less stress-tolerant species (Valiente-Banuet and Verdú 2013). Given the evolutionary conservatism of the functional traits involved in the recruitment process and the stronger dependence of recruits on canopy plants in stressful sites (Pérez-Navarro et al. 2024), the phylogenetic signal in networks from more arid environments is expected to be higher. Aridity is projected to increase globally (Dai 2013), leading to soil moisture decreases that could critically hamper plant recruitment. In this context, assessing how the phylogenetic signal in plant recruitment interactions varies with aridity can be useful to predict climate change effects on plant recruitment, as, for example,
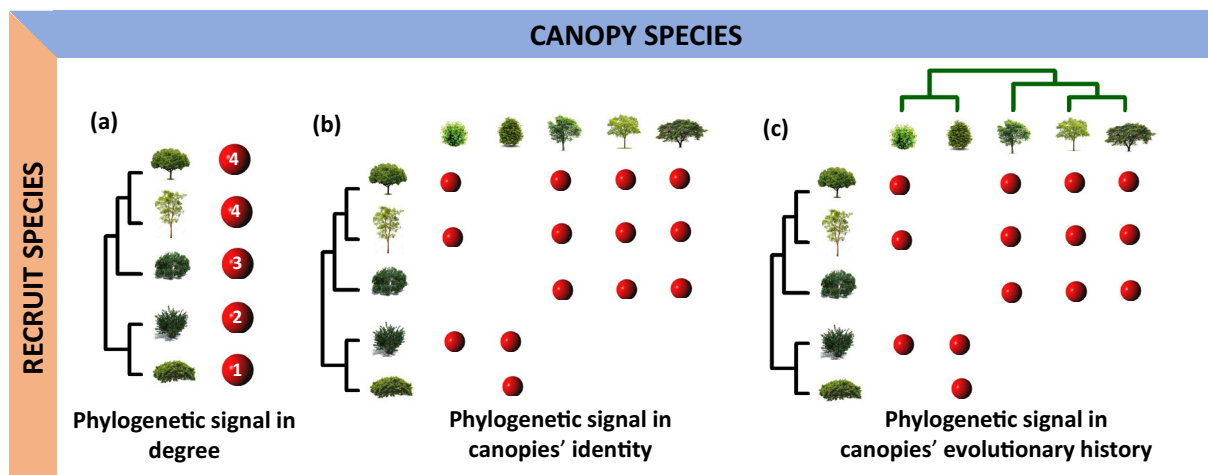
FIGURE 1 | Cartoon example of three different types of phylogenetic signals present in a recruitment network depicting the pairwise interactions between canopy plants (represented in columns) and the juvenile plants that recruit under them (represented in rows). These interactions are evolutionarily conserved when closely related recruits interact (a) with similar numbers of canopy species (i.e., phylogenetic signal in the number of partners, or in the specialisation of the interaction), (b) with taxonomically similar groups of canopy species (i.e., phylogenetic signal in canopies' identity) or (c) with evolutionarily similar groups of canopy species (i.e., phylogenetic signal in canopies' evolutionary history). Black phylogenies illustrate the evolutionary relations among recruiting species, while the green one shows the evolutionary relations among canopy species. The red numbered circles in (a) represent the specialisation of the recruitment interactions for recruits, while the red circles in (b) and (c) depict pairwise interactions between canopy and recruit species. Note that the only difference between panels (b) and (c) is the addition of phylogenetic information for canopy species.

phylogenetic redundancy may make plant communities more resilient to species or interaction losses.

In this study, we analysed the phylogenetic structure of 133 recruitment networks included in RecruitNet, a global database of recruitment networks (Verdú et al. 2023), that encompasses both temperate and tropical plant communities. Taking advantage of the broad range of climates and vegetation types of the available networks, we first asked whether the phylogenetic signal in recruits' interactions with canopy species is ubiquitous across plant communities. Our analyses spanned different dimensions of the recruitment niche (Figure 1) with the particular goal of assessing the relevance of the taxonomic identity and the phylogenetic history of the canopy species in explaining recruitment patterns. In addition, we analysed separately the phylogenetic structure of facilitation (i.e., positive interaction outcome for the recruit species), competition (i.e., negative interaction outcome for the recruit species) and neutral (i.e., the recruit species remains unaffected) subnetworks of the recruitment networks. Finally, we evaluated whether the phylogenetic signal in species interactions varies with aridity, under the expectation that more severe environmental conditions will lead to stronger phylogenetic signatures in the structure of the recruitment networks from more arid plant communities.

2 | Methods

2.1 | Recruitment Networks and Phylogenetic Trees

The recruitment networks were derived from the RecruitNet database, which comprises 135,210 observed canopy–recruit interactions from 143 plant communities across 23 countries

spanning all five continents. These communities represent a wide range of biomes and vegetation types in tropical and temperate regions (Figure S1; Verdú et al. 2023). Within each plant community, recruitment interactions were recorded by using one out of the following protocols: the RN protocol, in which all canopy–recruit interactions in a plot were recorded, the paired canopy-open protocol, which consisted of registering all recruiting individuals under a focal canopy and in a nearby open space, and the georeferenced plot protocol, in which canopy–recruit interactions were inferred from georeferenced plants (Verdú et al. 2023).

To obtain a phylogeny describing the evolutionary relationships among all the species (i.e., canopies and recruits) included in the RecruitNet database ($N = 3280$), we used the R package 'V.PhyloMaker2' (Jin and Qian 2022), which allows to obtain dated phylogenies from large species lists. As this approach needs species names from the list to match tip names from the chosen mega-phylogeny within the package, we first corrected some name spelling from the original database, and also checked for accepted names according to World Flora Online (WFO 2023), given that we chose to use the mega-phylogeny whose species names were standardised according to this database (i.e., GBOTB.extended.TPL.tre; Jin and Qian 2022; Smith and Brown 2018). This R package also allows to format the input file with the species' list so as to include phylogenetic affinities extracted from the literature for those species not originally represented in the mega-phylogeny, a procedure that is highly recommended to improve the resulting phylogeny (Jin and Qian 2019). Accordingly, we compared the list of genera in RecruitNet with the genera included in the mega-phylogeny, and found that 120 genera listed in RecruitNet (8.7%) were not represented in the mega-phylogeny. We searched in the literature for phylogenetic

affinities for these genera (Table S1), and formatted the input file so as to include this information. The phylogeny including all species in RecruitNet was then obtained by running the phylo.maker function with this input file, with the options 'S3' for inserting absent species and 'nodes.info.1.TPL' for dealing with nonmonophyletic genera (Jin and Qian 2019; Qian and Jin 2021). To evaluate if phylogenetic uncertainty could affect the results, we also built alternative phylogenies by considering scenarios S1 and S2 (Jin and Qian 2019), and a set of fully resolved phylogenies in which the soft polytomies were randomly resolved. For the latter, we generated 100 completely resolved phylogenies using the 'fix.poly' function from the R package 'RRphylo' (Castiglione et al. 2020), which resolves randomly the polytomies adding non-zero length branches to each new node, with new branch lengths being equally partitioned below the dichotomised clade. The magnitude of the correlation between sets of phylogenetic signals obtained using different input phylogenies was taken as a measure of the sensitivity of our analyses to the assumption of different phylogenetic hypotheses.

2.2 | Phylogenetic Signal

In each recruitment network, we estimated the phylogenetic signal in recruitment interactions by assessing whether closely related recruiting species have similar recruitment niches. The similarity in the recruitment niche was quantified by estimating the specialisation of the interactions (i.e., the number of canopy species associated with each recruiting species; Figure 1a), and also by characterising the niche in terms of the taxonomical and evolutionary composition of the set of canopy plants (Figure 1b,c). For the latter, we used two indices of ecological dissimilarity, namely, the weighted Jaccard index (Legendre and Legendre 1998; Rezende et al. 2007) and the weighted Unifrac index (Lozupone and Knight 2005). The Jaccard index considers the taxonomic identity (identity hereafter) of the canopy species (Figure 1b), while the Unifrac index takes into account the phylogenetic distance between sets of canopy species (Figure 1c). More specifically, the Unifrac distance between two recruited species quantifies the ratio of the evolutionary history of the set of canopy plants unique to each recruited species compared to the total amount shared by both (i.e., the proportion of unshared branch lengths). By using both indices, we aimed to capture two scenarios: canopy–recruit interactions where recruitment patterns are associated with the identity of the canopy species, and interactions in which the evolutionary history of the set of canopy species explains recruitment patterns. For each network, we obtained the phylogenies for canopy and recruit species by pruning the overall RecruitNet phylogeny, and the interaction matrices by extracting the interactions recorded for each network from the RecruitNet database. We discarded those networks including less than three canopy or recruit species ($N = 10$ nets); the resulting networks contained from 3 to 541 species. The phylogenetic signal in canopy–recruits' interactions was then estimated for each of the 133 networks by performing Mantel correlation tests between phylogenetic and ecological distance matrices, using the R function 'phylosignal_network' from the R package 'RPANDA' (Morlon et al. 2016). For the ecological distance matrices, we considered both Jaccard and Unifrac indexes, which were weighted by interaction frequencies to account for

stochastic processes related to species' abundances (Alcántara, Garrido, and Rey 2019). When estimating the phylogenetic signal in the degree of the recruit species, we used ecological distance matrices that included pairwise degree differences (Perez-Lamarque et al. 2022). Mantel tests were performed by estimating Pearson correlation coefficients, which represent the sign and strength of the phylogenetic signal. Positive correlation coefficients (i.e., positive phylogenetic signals) indicated that closely related recruits displayed more similar recruitment niches than random expectations, while negative correlation coefficients (i.e., negative phylogenetic signals) indicated that closely related recruits had more divergent recruitment niches than randomly expected. The statistical significance of the phylogenetic signal was assessed by comparing the observed values with null distributions obtained by randomising the ecological distance matrix. As the presence of phylogenetic signal in the number of interacting species (i.e., species degree; Figure 1a) may affect the estimation of the phylogenetic signal (Rezende et al. 2007), the statistical significance of the phylogenetic signals accounting for the taxonomic composition and evolutionary history of the canopies was assessed following a conservative approach proposed by Perez-Lamarque et al. (2022). This consisted of comparing the observed Mantel correlations with null distributions generated by randomising the canopies' identities and keeping the number of interacting species constant. Positive phylogenetic signals were considered statistically significant when they were higher than 95% of the random correlation values, and negative significant signals when they were lower than 95% of the random values. Furthermore, we assessed whether the size of the networks or the sampling method used for scoring canopy–recruit interactions (Verdú et al. 2023; see above) could affect the phylogenetic signals obtained by running linear regressions; network size was estimated as the number of canopy species multiplied by the number of recruiting species. Finally, we analysed biases in the phylogenetic signals associated with spatial autocorrelation by estimating Moran's I autocorrelation indexes. For this, we constructed geodesic distance matrices with the R package 'geodist' (Padgham 2021), and obtained the autocorrelation indexes by running the 'Moran. I' function from the R package 'ape' (Paradis and Schliep 2019).

Given that the phylogenetic structure of canopy–recruit interaction networks may depend on the type of interaction, we also analysed the phylogenetic structure separately for subnetworks integrated exclusively by links involving facilitation (i.e., positive outcome for the recruit), competition (i.e., negative outcome for the recruit) and neutral interactions (i.e., the recruit remains unaffected by the interaction). It should be noted that we are not considering the recruitment interactions in terms of reciprocal effects but only in terms of the effects of the canopies on recruiting plants. In the plant–plant interaction literature, it is common to use the terms 'facilitation' and 'competition' to refer to the positive and negative effect of one species on another, respectively, regardless of whether the effect is reciprocal between species or not (e.g., Kinlock 2019). Then, we categorised each observed canopy–recruit interaction contained in the 133 networks as positive, negative or neutral through chi-square tests assessing whether the number of recruits under each canopy species was statistically greater, lesser or similar to the expectation determined by canopy coverage. Given that canopy species modify the

microenvironmental conditions (e.g., soil parameters) in the recruiting potential spaces, we assumed that the associations between canopy and recruiting species were not due to shared abiotic preferences.

Using this information, we pruned the RN for every study site to obtain purely facilitative, competitive and neutral interaction subnetworks. Phylogenetic signal in these subnetworks was then estimated as previously described. To assess whether the magnitude of the phylogenetic signals depended on the type of interaction involved (i.e., facilitative, competitive or neutral), we ran mixed linear models with type of interaction considered as a fixed effect and study site as a random effect. In addition, we tested whether the frequency of positive and negative signals (i.e., ecological distance increasing or decreasing with increasing phylogenetic distance respectively) was related to the type of interaction by means of chi-squared tests.

Finally, we evaluated whether environmental stress could influence the phylogenetic structure in recruitment patterns. To measure environmental stress, we used the aridity index, a commonly used indicator of water availability for plants. This index is calculated as the ratio of precipitation to potential evapotranspiration, and thus, larger index values indicate lower aridity. We downloaded aridity index data from a raster file with a resolution of 30 arc-seconds provided by Chelsa V2.1 (Karger et al. 2021), and extracted the aridity index for each study site with the R package 'raster' (Hijmans 2023). We then analysed whether the phylogenetic signal in recruits' interactions with canopies varied with the aridity index (expressed as 1-aridity index, to facilitate interpretation), for both ecological distances and for positive and negative phylogenetic signals separately. All analyses were performed using R version 4.3.3 (R Core Team 2024).

3 | Results

The specialisation of the interactions between recruits and their canopies (i.e., the degree of the recruit species) was phylogenetically conserved in 7.52% of the analysed networks. In addition, we detected significant phylogenetic signals in the interactions of recruits with canopies in 12.1% of the networks when canopies' identity was taken into account and in 10.6% of the networks when the canopies' evolutionary history was considered (Table 1). We found that the ecological distances both increased (i.e., positive signal) and decreased (i.e., negative signal) with

increasing phylogenetic distances (Figure 2). The strength of the signals (i.e., absolute values) was greater in plant communities where ecological distances increased with increasing phylogenetic distance (Figure 2; and Table S2), although the difference in strength was statistically significant only when the evolutionary history of the canopy species was taken into account (estimate $\pm$ SE: 0.009 ± 0.015; $p = 0.562$, and estimate $\pm$ SE: 0.062 ± 0.019; $p = 0.002$, for analyses considering the canopy's identity and their evolutionary histories respectively). The phylogenetic signals estimated using these two types of ecological dissimilarity were highly correlated ($r = 0.73$, $p < 0.001$), with higher (absolute) values obtained when accounting for the canopies' evolutionary history for both positive and negative phylogenetic signals (Figure 3). Finally, the estimates of phylogenetic signals were neither affected by phylogenetic uncertainty (Table S3a,b), nor by the spatial location of the plant communities, the size of the networks or the field sampling methodology applied (Table S4).

When the recruitment networks were decomposed into their three interaction types (i.e., facilitation, competition or neutral interactions between canopies and recruits), we found that the magnitude and sign of the signals were independent of the interaction type (Table S5 and Figure S2). However, the facilitation and competition subnetworks exhibited the highest percentages of significant signals (Table 1). Interestingly, the percentages of networks exhibiting significant signals were above the 5% expected by chance in the facilitation and competition subnetworks, while in the neutral subnetworks, this percentage remained below that threshold. Furthermore, the correlation between the phylogenetic signals estimated using the two types of ecological dissimilarity was highest for neutral interactions ($r = 0.96$ [0.95, 0.98]), followed by competitive ($r = 0.86$ [0.74, 0.93]) and lastly by facilitative interactions ($r = 0.65$ [0.51, 0.76]). The greater uncoupling between both types of phylogenetic signals (i.e., lower correlation) found in the facilitation networks (and to a lesser extent in competition ones) reflects stronger signals obtained when accounting for the evolutionary history of the canopy species (Figure S3). This indicates that closely related species can often perform similar roles as canopy species (i.e., phylogenetic redundancy).

The percentages of facilitative and competitive interactions significantly increased with increasing aridity levels (1.028 ± 0.086, $p < 0.005$ and 1.724 ± 0.380, $p < 0.005$ for facilitative and competitive interactions respectively), while, accordingly, the percentage of neutral interactions significantly

TABLE 1 | Percentage of statistically significant phylogenetic signals for the complete recruitment networks (i.e., including all recruitment interactions irrespective of their interaction type), and for facilitation, competition and neutral subnetworks.

	Canopies' identity	Canopies' evolutionary history
Complete networks	12.2% (16/132)	10.6% (14/132)
Facilitation subnetworks	13.2% (11/83)	10.3% (9/87)
Competition subnetworks	11.4% (4/35)	11.4% (4/35)
Neutral subnetworks	2.3% (2/85)	2.3% (2/87)

Note: Phylogenetic signals were estimated based on either the identity or the evolutionary history of the sets of canopy species as measures of ecological dissimilarities. The number of networks with significant signals out of the total number of networks is indicated within brackets. One of the networks ('Tojo') was excluded from all analyses because of its extreme but nonsignificant phylogenetic signals. In some subnetworks (i.e., six subnetworks), the phylogenetic signal could not be estimated because of identical interaction patterns among species.
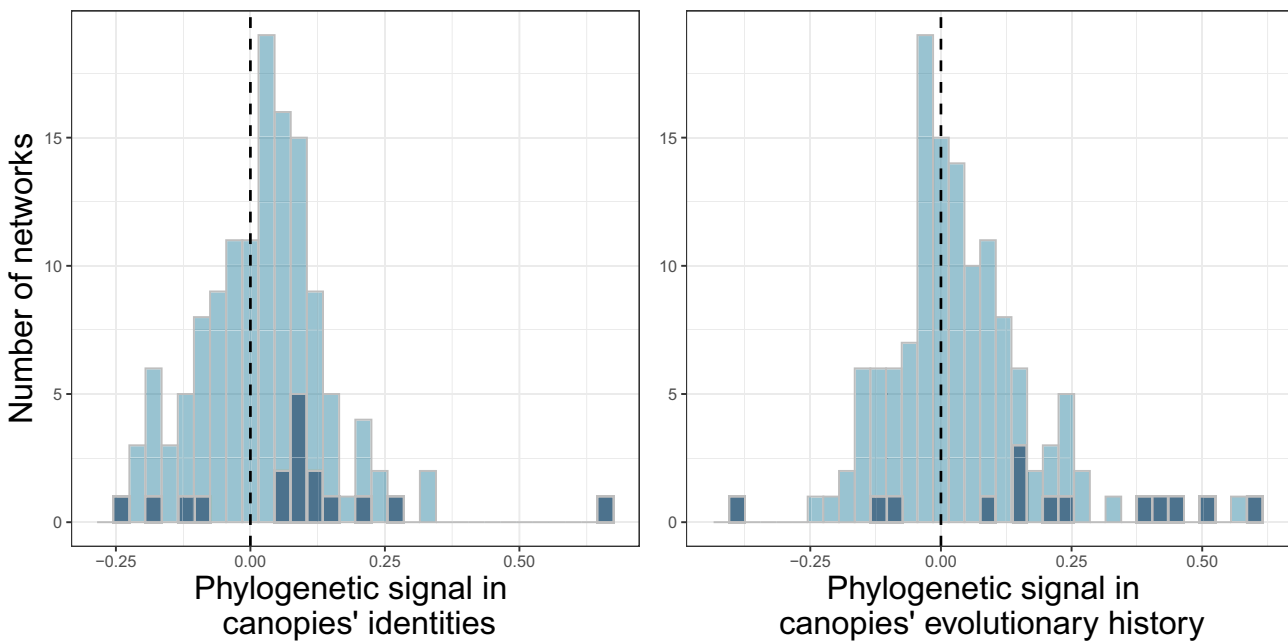
FIGURE 2 | Frequency distribution of phylogenetic signals in recruits' interactions with canopies, estimated considering the canopies' identity (left panel) and the canopies' evolutionary history (right panel) as measures of ecological dissimilarity, for 132 canopy–recruit interaction networks. The number of networks with significant phylogenetic signals is indicated with dark blue bars. One of the networks ('Tojo') was excluded because it yielded extreme yet nonsignificant phylogenetic signals probably due to its small size. The phylogenetic signals are skewed towards positive values (i.e., ecological distances increasing with increasing phylogenetic distances) for both ecological dissimilarity measures (skewness = 0.937 and skewness = 1.057 for the left and right panels respectively).

decreased with increasing aridity (-1.163 ± 0.089, $p < 0.005$). Overall, the phylogenetic signal in recruits' interactions was stronger in networks from more stressful environments (Figure 4). Specifically, the magnitude of positive phylogenetic signals increased with aridity levels in analyses considering both the canopies' identities (estimate $\pm$ SE = 0.079 ± 0.025, $p = 0.002$) and their evolutionary histories (0.100 ± 0.035, $p = 0.005$). However, this effect vanished for negative signals, for both ecological similarity approaches (-0.038 ± 0.022, $p = 0.087$ and -0.045 ± 0.026, $p = 0.081$ when the identity of the canopy species and their evolutionary histories were considered respectively).

4 | Discussion

Plant recruitment is one of the most important bottlenecks for population and community dynamics because it depends on multiple processes (i.e., seed dispersal, predation and germination) that may limit plant establishment in a safe site (Terborgh et al. 2014). In addition to the stochasticity associated with these processes, surrounding adult plants may also affect establishment success, adding a deterministic component to recruitment which can be associated with evolutionary and environmental effects (Alcántara et al. 2018). Our comprehensive analysis on recruitment networks, which spans a diverse range of climates and vegetation types, has found that, despite the high level of stochasticity, recruitment niches are phylogenetically conserved in more networks than expected by chance (i.e., more than 10% of the networks displayed a significant phylogenetic signal). In particular, the phylogenetic signal in recruitment interactions

was more positive and stronger in communities from harsher environments.

The recruitment networks analysed varied in the strength and sign of the phylogenetic signal in the interactions. The distribution of phylogenetic signals showed a slight skew towards positive signals; in those networks, closely related species tend to recruit under the same or under closely related canopies, indicating that their recruitment niches are evolutionarily conserved (Valiente-Banuet and Verdú 2007). A fewer number of networks showed a negative signal suggesting that, in these communities, closely related species recruit under different or phylogenetically distant groups of canopy species. Such a negative signal may reflect divergent evolution of recruitment niches that might have been driven by past resource competition among recruiting species (Elias, Fontaine, and Frank Van Veen 2013; Martín González et al. 2015). However, this result must be interpreted with caution, as the occurrence of false positives for negative phylogenetic signals estimated with Mantel tests seems to be frequent (Perez-Lamarque et al. 2022). In most networks (> 85%), however, the magnitude of the phylogenetic signal was close to zero. This pattern agrees with previous studies examining the phylogenetic signal in pollination and seed dispersal interactions, which found a low frequency of significant phylogenetic signal in the ecological interactions involving plants (Aizen et al. 2016; Rezende et al. 2007). The lack of a phylogenetic signal in most recruitment networks may indicate that recruitment interactions depend ultimately on stochastic processes, that recruitment-related traits show high environmental plasticity or, alternatively, that deterministic processes underlying positive and negative phylogenetic signals
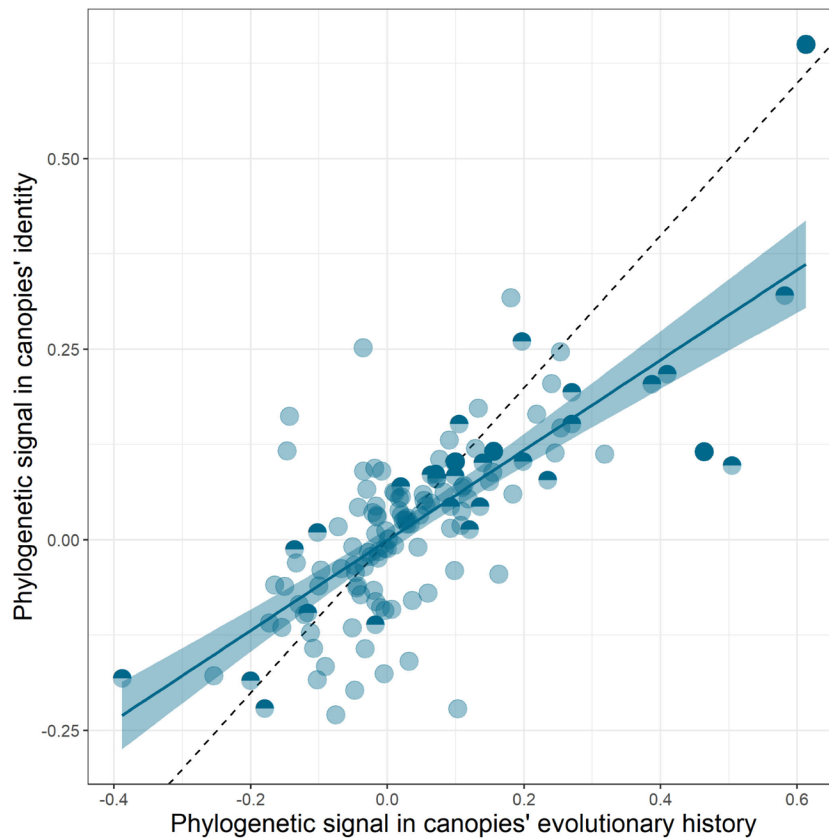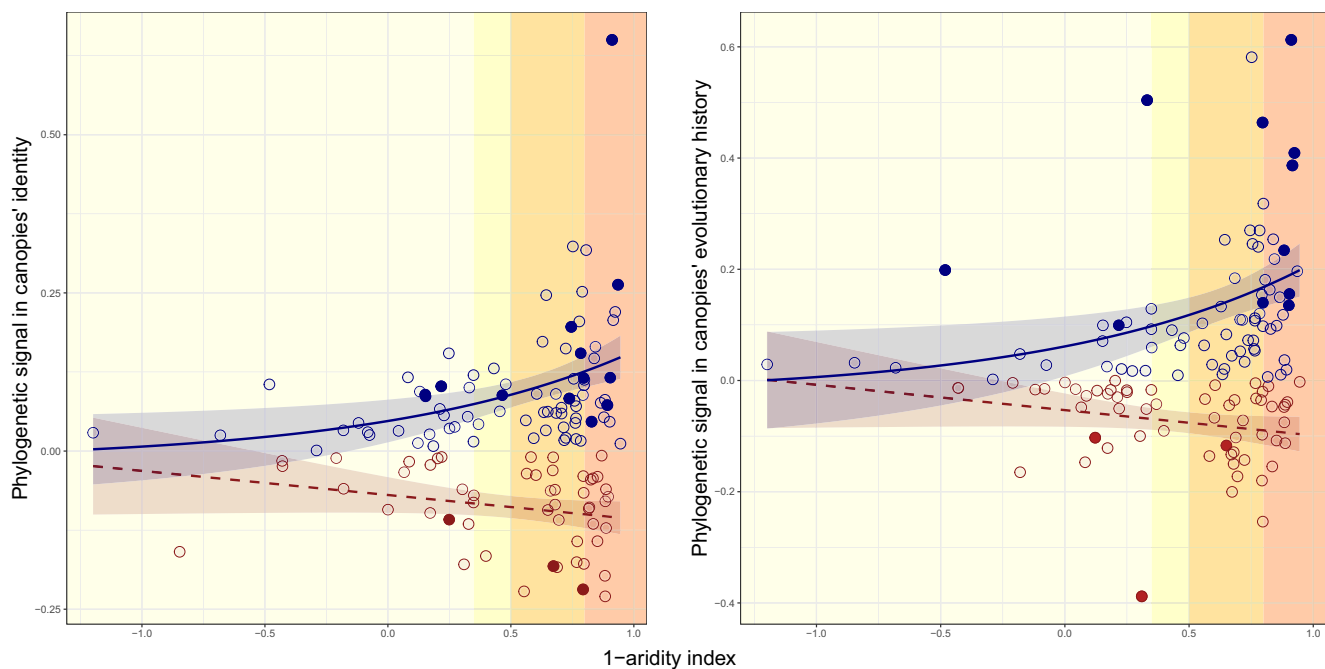
FIGURE 3 | Relationship between the phylogenetic signals obtained by considering either the canopies' identity or their evolutionary history as measures of ecological dissimilarity. Light blue symbols represent networks with nonsignificant phylogenetic signals, dark blue symbols networks with significant phylogenetic signals for both ecological dissimilarity indexes and the bicoloured ones represent those networks in which phylogenetic signals were significant for one of the two ecological dissimilarity indexes used. The solid line represents the correlation between the phylogenetic signals obtained with both ecological dissimilarity measures, the shaded area the 95% confidence interval around the correlation line and the dotted line the theoretical perfect correlation line passing through the origin (i.e., $y = x$).

are counterbalancing each other. Under an evolutionary perspective, the absence of phylogenetic signal in recruitment interactions suggests that canopy plants are not exerting selective pressures on the traits of the recruiting species or, alternatively, that these traits are subject to conflicting selective pressures (Cirtwill et al. 2020). In fact, conflicting selective pressures may arise because, for example, traits that are adaptive under some environmental conditions may be maladaptive when conditions change (Tielbörger and Kadmon 2000). While it is true that recruitment interactions between plants have not generated adaptive traits as evident as those of other interactions, such as pollination, seed dispersal or herbivory, there is evidence that certain traits can evolve in response to the interaction between canopies and recruiting plants (Verdú et al. 2021). In fact, facilitation is promoted by trait-matching mechanisms through which nurse and facilitated species avoid phenotypic overlap (Navarro-Cano et al. 2021). Finally, we cannot rule out the possibility that we underestimated the number of significant phylogenetic signals due to the moderate statistical power of the Mantel tests. Despite this limitation, this approach has proven to be the preferred method for estimating phylogenetic signal in interspecific interactions (Perez-Lamarque et al. 2022).

As it occurs in other ecological interactions, our study revealed that phylogenetically driven deterministic processes

can influence recruitment interactions, as a significant phylogenetic structure was detected in more networks than expected by chance. Interestingly, the analysis that took into account the evolutionary history of the canopy species proved more effective than that considering the canopies' taxonomic identities in explaining the recruitment interaction patterns (Figures 3 and S3; Bergamini et al. 2017). This indicates that the role of a canopy plant in the community can be acquired by another evolutionarily related plant, probably because both species share similar traits due to common ancestry. This finding has important implications for network stability in terms of recruitment resilience to disturbances; in these networks, recruitment patterns will probably not be disrupted if the interactions with some canopy species are lost, because recruits can rewire (i.e., switch partners) with other phylogenetically close canopy species (Sánchez-Martín, Verdú, and Montesinos-Navarro 2023).

Previous studies have shown that the strength of the phylogenetic signal in interaction networks may depend on the interaction outcome, with stronger phylogenetic signals found in antagonistic networks that are composed of species that produce a negative effect over other species, than in mutualistic ones, where both interacting partners obtain a benefit (Fontaine and Thébault 2015; Maliet, Loeuille, and Morlon 2020; Rohr and Bascompte 2014). Recruitment

FIGURE 4 | Relationship between the phylogenetic signal in recruitment interactions and aridity, considering either the identity of canopy species (left panel) or their evolutionary history (right panel). The aridity level was quantified with the aridity index (precipitation/potential evapotranspiration), which is here expressed as 1-aridity index to facilitate interpretation (i.e., increasing index values represent increasing levels of aridity). Networks with a positive phylogenetic signal in recruits' interactions (i.e., ecological distances increasing with increasing phylogenetic distances) are coloured in blue, and those with a negative phylogenetic signal (i.e., ecological distances decreasing with increasing phylogenetic distances) are coloured in red. Solid circles represent networks with significant phylogenetic signals. The solid blue lines depict significant associations between the phylogenetic signal and the aridity level, while the dashed red lines show nonsignificant associations. The shaded areas represent 95% confidence intervals around the regression lines. The background colours illustrate the discrete aridity categories defined in UNEP (1997); those colours that are closer to red hues indicate higher aridity levels.

involves different types of interactions, as recruits can profit from the interaction with canopies (i.e., facilitation), be negatively affected (i.e., competition) or remain unaffected by the interaction (Alcántara et al. 2018; Valiente-Banuet and Verdú 2008). Even if the interaction outcome for the recruit species can vary, we did not find evidence that the magnitude or sign of the phylogenetic signal differed for facilitative, competitive or neutral interactions. However, the number of subnetworks that displayed a statistically significant phylogenetic signal was greatest in facilitation and competition networks, and was below the 5% random expectation threshold in neutral networks. Interestingly, the phylogenetic signals estimated using the two measures of ecological dissimilarity were highly correlated in neutral networks, which indicates a negligible role of the canopies' evolutionary history as a driver of neutral interactions between recruits and canopies. Based on these findings, we propose that evolutionary history may play a significant role in shaping recruitment interactions, particularly when canopy species have a substantial impact on the performance of recruits, either through facilitation or competition.

Furthermore, we found that the phylogenetic signal in the interaction networks varied along an environmental stress gradient, but only in those communities in which closely related species were recruited under more closely related groups of canopy species (i.e., in those communities with a positive phylogenetic signal). Previous studies in other ecological interactions

have reported associations between phylogenetic signals and environmental heterogeneity (e.g., Corro et al. 2021; Krasnov, Shenbrot, and Khokhlova 2022), but the phylogenetic signal in plant recruitment interactions has never been compared across plant communities on a global scale. Our extensive dataset shows that the phylogenetic signal was more positive in more arid plant communities, indicating that the plant's evolutionary history plays a more significant role in shaping recruitment interactions when environmental conditions get harsher. *This supports the findings by Valiente-Banuet et al. (2006), which demonstrated that nurse plants were essential for maintaining the niches of ancient plant lineages as conditions became more arid. Facilitated species rely heavily on these nurse plants, as their niches would not exist without them, which explains their phylogenetic connections. Altogether, these results* align with earlier research that examined recruitment patterns in semiarid Mediterranean communities, which revealed a significant phylogenetic signal in species interactions (Alcántara, Garrido, and Rey 2019; Verdú and Valiente-Banuet 2011). It has to be pointed out, however, that a large amount of variation remained unexplained in our analysis. This is likely due to the extensive variety of plant communities we examined, which spanned diverse biogeographic areas and are, therefore, expected to differ in factors beyond aridity.

The challenging conditions present in arid environments have driven the evolution of specific traits in plants that enable them to tolerate such conditions (Basu et al. 2016). Additionally, these

harsh environments lead to an increased occurrence of facilitative interactions (López et al. 2016), which typically enhance the fitness of the recruiting species. At the same time, canopy species may also obtain benefits from these interactions (Montesinos-Navarro et al. 2019). Stronger phylogenetic signals are indicative of interaction specialisation and, therefore, higher specialisation in canopy–recruit interactions may have evolved in stressful environments because these conditions intensify the need for recruits to match the traits of canopy species for survival. This could explain the greater phylogenetic signal found in networks from more arid environments, as interaction specialisation has been associated with stronger phylogenetic signals (Maliet, Loeuille, and Morlon 2020; Shefferson et al. 2019). However, only an analysis of functional trait variation could help to understand the underlying mechanisms explaining the observed aridity effect on the phylogenetic architecture of the networks. Even if we cannot unravel the processes leading to the differences in the phylogenetic signal among the analysed plant communities, our study reveals an emerging pattern that has important implications regarding plant communities' responses to the ongoing climate crisis. Aridity has increased in many areas in the last decades, and has been predicted to keep increasing during this century (Dai 2013). Plant recruitment is, therefore, expected to be hampered due to an increasing water deficit. According to our results, in drier plant communities this effect is likely to be less harmful, because of the greater phylogenetic signal present in the recruitment patterns. In these communities, if some canopy species disappear, recruitment will probably not be severely compromised because of phylogenetically driven rewiring.

In summary, our study reveals that, even if recruitment can be strongly influenced by stochastic processes, it can also be driven by the plants' evolutionary history, especially under harsh environmental conditions. In particular, the effect of evolutionary history in shaping ecological interactions becomes more prominent when recruitment interactions are more tightly intertwined, as is the case with facilitation and competition-mediated recruitment. More broadly, we demonstrate the significance of examining diverse aspects of ecological niches, as such an approach can unveil additional insights into the functional roles played by interacting species.

Author Contributions

M.V. and G.G. conceived the idea; J.M.A., J.L.G., A.M.N., and M.V. coordinated the collection of data; G.G. ran the statistical analyses and wrote the first draft of the manuscript; all authors contributed to subsequent revisions.

Acknowledgements

Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

Data on canopy–recruit interactions used in this paper are already publicly available in Verdú et al. (2023) and also in Zenodo at https://doi.org/10.5281/zenodo.6567608. All the networks, phylogenetic tree and environmental data as well as scripts to run the analyses are available in Zenodo at https://doi.org/10.5281/zenodo.10775506.

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Supporting Information

Additional supporting information can be found online in the Supporting Information section.